Journal of Environmental Management 236 (2019) 17–24

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

The importance of fire season when managing threatened plant species: A long-term case-study of a rare *Leucopogon* species (Ericaceae)

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ARTICLE INFO

Keywords:
Fire ecology
Plant functional traits
Fire interval squeeze
Mediterranean versus non-Mediterranean climates
Physiological dormancy
Seed ecology

ABSTRACT

Implemented burns are a primary source of fire in natural systems and occur outside of the wildfire season. However, the impacts of fire season shift on native plant species are rarely studied. Understanding fire season effects are particularly important for managing threatened species, which are often the focus of managed burns. To assess the impacts of fire seasonality and identify potential limiting traits, I studied the threatened *Leucopogon exolasius* and two common congeners, all of which persist via fire-driven population dynamics. All species were monitored over a 16 year period to assess seedling survival, growth and primary juvenile period after fire. For L. *exolasius* and the common *L. esquamatus*, comparisons of survival, growth and maturation were made after winter and summer fires, to assess the effects of season of burn. A key difference was found in primary juvenile period, which was exceptionally long for *L. exolasius* (> 11 years for 80% of the population to flower) compared to the common congeners (3.2–7.57 years). Seasonal seed dormancy mechanisms meant that winter fires delayed emergence, leading to increases in primary juvenile period for both species. A long primary juvenile period may limit *L. exolasius* population persistence because plants are more likely to be killed by subsequent fire before maturation, while seasonal dormancy cues is a trait that would exacerbate the effects of this interval squeeze. In fire-prone systems, fire frequency is the key factor assumed to drive persistence, however, interactions with fire season can influence recruitment success. There are scant data on recruitment variation in response to fire seasonality, a factor that may have broad implications for rare and common species with seasonal germination requirements.

1. Introduction

Fire regime components include frequency, intensity (or severity) and season (Whelan, 1995; Hammill et al., 2016). The impact of fire frequency has been the focus of numerous studies, with a decrease in the intervals between fires limiting to obligate-seeding shrub species with long primary juvenile periods (e.g. Santana et al., 2014). Projected changes to climate could exacerbate this interval squeeze (Enright et al., 2015; Fairman et al., 2016). Nevertheless, other fire regime factors, such as season and severity, can also undoubtedly affect plant population persistence and recovery (e.g. Ooi et al., 2004, 2014; Liu et al., 2005; Ooi, 2010; Céspedes et al., 2014; Hammill et al., 2016) but there are few empirical studies measuring these effects over long time periods. Furthermore, managed burns are a primary source of fire in natural systems and are shifting fire season away from the peak time of natural wildfire. Understanding fire seasonality effects are particularly important for managing threatened species, however, the impacts of fire season shift on native plat populations are rarely studied.

In many fire-prone regions, fire causes plant mortality and successful recruitment is restricted to the post-fire environment. For perennial species from such habitats, this means that long-term studies are required to understand population dynamics, because inter-fire periods can last for decades (Whelan, 1995; Menges and Quintana Ascencio, 2004), and shifts between life-history stages may run over similar time scales. For example, gaining an estimate of primary juvenile period is important for determining the fire frequency that a species may be able to persist under (Keith, 1996). This can take from between two and 10 (or more) years for species in areas such as temperate Australia (Benson, 1985; Burrows et al., 2008; Kubiak, 2009), where fire return intervals range from approximately seven to 30 years (Bradstock and Gill, 2001; Lucas et al., 2007). Shorter term correlates of these measurements, such as size-class distributions for population age structure (e.g. Ooi et al., 2007), may be more easily achievable but do not provide the necessary resolution for parameterising predictive population models. However, long-term demographic studies, beyond a few years, are extremely rare.

Demographic studies are valuable for both the management of rare and threatened plant species, and predicting persistence (Schemske

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https://doi.org/10.1016/j.jenvman.2019.01.083
Received 28 June 2018; Received in revised form 21 January 2019; Accepted 23 January 2019
Available online 31 January 2019
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et al., 1994; Menges et al., 2006; Keith et al., 2008). Comparative studies that investigate the biology of ecologically similar rare species and common congeners can help to detect possible limiting factors within the rare species (Kunin and Gaston, 1993; Bevill and Louda, 1999; Mattana et al., 2010). Although it is unlikely that generalisations exist regarding the causes of rarity (Gaston, 1994), insights gained from data collected in comparative studies are particularly useful for the conservation of threatened species and the detection of broader ecological patterns (Bevill and, Louda, 1999; Lavergne et al., 2004). These broader patterns may help to identify traits that could be limiting under changing environmental conditions, for both rare and common species, and provide insights to the evolutionary development of specific traits.

Regeneration from seeds is necessary for short-term regeneration and long-term persistence in fire-prone regions (Whelan, 1995; Bond and van Wilgen, 1996; Ooi et al., 2014). Plants that do not resprout, known as obligate-seeding species, are particularly dependent on recruitment from stored seed. As such, critical factors for the persistence of these species, and potential causes of rarity, are often related to seed ecology and recruitment stages (Burne et al., 2003; Risberg and Granström, 2014). Additionally, fire is the predominant driver of plant population dynamics in these regions and aspects of the fire regime itself needs to be considered as a potential contributor to rarity (Burne et al., 2003).

An increased use of managed fires, in addition to climate change, is causing a shift from current peak fire seasons, in addition to increasing the frequency of fire (McLoughlin, 1998; Williams et al., 2001; Cary et al., 2006; Enright et al., 2015). The threats caused by altered fire regimes may not only affect the persistence of those plant species that are already threatened with extinction, but also of many common species. Such common species may be at risk because they possess traits that have little plasticity in relation to projected changes. The most inflexible traits are likely to be those that are not adapted to current environmental conditions, but have ecologically fit well enough to have persisted. Evidence suggests that species composition within ecological communities may be strongly influenced by the relative abilities of species to cope with climate-driven changes (Suttle et al., 2006).

There is growing evidence that rates of extinction of plant species are increasing, across local and regional scales (Thomas et al., 2004a; Thuiller et al., 2005). This rate is influenced by human population growth, and the associated escalating demands on resources and climate-driven changes (Gaston, 2005; Hahs et al., 2009). Species most at risk by the threat of extinction are those that are already rare, and therefore already limited in abundance and/or distribution (Gaston, 1994; Wilson et al., 2004). Understanding the possible anthropogenic and ecological causes of rarity are therefore crucial to designing and implementing conservation actions. In this study, I investigated post-fire recruitment and development over a 16 year period for the species *Leucopogon exolasius* (F. Muell.) F. Muell. ex Benth. and the closely related common congeners *L. setiger* R. Br. and *L. esquamatus* R. Br. The demographic parameters following regeneration were compared between species in order to determine any potential causes of rarity for one of them, the threatened *L. exolasius*. All three species inhabit the fire-prone temperate sandstone vegetation around the Sydney region in south-eastern Australia, occurring on similar soil types and in similar micro-climates. The vegetation here is adapted to fire and there is a mean natural wildfire return interval ranging from approximately 14 to 20 years, a similar interval to shrublands in Mediterranean-climate regions in southwestern Australia (Miller and Murphy, 2018). Fires occur primarily in the hot late spring and summer periods (approximately November to February). The Sydney sandstone basin is one of several centres of high species richness and endemism on the Australian continent (Crisp et al., 2001), but also highly urbanised. Prescribed fires are therefore implemented regularly to reduce fuel loads and protect assets, as well as for ecological purposes such as the conservation of biodiversity (Penman et al., 2011).

Because limited abundance or distribution of plant species are unlikely to be attributed to a single factor, investigations into several critical biological traits and life-history stages are the most likely to highlight limiting processes (Rabinowitz et al., 1984; Bevill and Louda, 1999). Part of the benefit of using a small number of species in a comparative study, is that a larger number of factors may be examined with relative ease, and species can also be more easily selected to control for phylogenetic relatedness (Kunin and Gaston, 1993; Walck et al., 2001). Additionally, understanding demographic responses to environmental disturbance is crucial in habitats situated on the urban interface where the numbers of implemented fires are increasing (McLoughlin, 1998) and climate change is projected to drive changes to fire season and frequency (Williams et al., 2001; Cary et al., 2006; Enright et al., 2015). I therefore assessed the demographic responses measured in the context of the fire regime to identify potential limiting traits. Specifically, I wanted to address the following questions:

(1) How do key life-history stages of the three *Leucopogon* study species differ, and what are their responses to the fire regime, particularly season?
(2) Can predicted changes to the fire regime potentially affect the persistence of the rare or common species studied?
(3) Are there any identifiable factors that limit *Leucopogon exolasius*?

2. Materials and methods

2.1. Study species and sites

The Ericaceae family occurs in a number of habitats throughout the world floras including in South Africa and the Mediterranean Basin (Ojeda et al., 1997). In Australia, members compromise a significant part of the understorey in fire-prone plant communities. *Leucopogon* (Ericaceae) is a large genus consisting of about 230 species. This fire-prone region of south-eastern Australia contains approximately 2000 plant species (Auld et al., 2000), and unlike its Mediterranean-type climate counterparts, has an aseasonal rainfall climate with no pronounced dry season, which may have consequences for the post-fire recovery of species with innate seasonal germination requirements (Ooi, 2010). The three study species are all obligate-seeding woody shrubs with soil-stored seed banks (Ooi et al., 2006a,b; 2007). Although they do not co-occur at the same sites, they inhabit adjoining heath and woodland vegetation types, and have overlapping ranges. *Leucopogon* fruit are drupes and fresh exocarps of both *L. exolasius* and *L. setiger* are fleshy, while the endocarp is hard and lignified. *Leucopogon esquamatus* exocarp is papery and the endocarp comparatively more fibrous than hard (Ooi et al., 2006a).

Leucopogon exolasius is an erect shrub that grows to approximately 2 m tall, and is a threatened species listed as 'vulnerable' both under the national Australian *Environment Protection and Biodiversity Conservation Act* (1999), and under the state of New South Wales (NSW) *Threatened Species Conservation Act* (1995). The species is endemic to the southern Sydney region of NSW and is restricted to approximately 14 known populations. It occurs in woodlands, and is restricted particularly to riverbank areas punctuated with outcropping sandstone. *Leucopogon setiger*, morphologically very similar to *L. exolasius*, is an erect shrub also approximately 2 m tall, and is distributed more widely (Table 1), extending from the central western slopes of NSW to the coast. It is found in woodlands and open forest. *Leucopogon esquamatus* is a slender shrub, which grows to approximately 1 m tall. It is also widespread, occurring from the coast to the mountains (as for *L. setiger*), but extending south into the states of Victoria and Tasmania (Table 1). It occurs in heath, woodlands and open forests. Taxonomy follows Harden (1992). Geographic distribution of each species were calculated using IUCN (2012) criteria for extent of occurrence, which is defined as the area contained within the shortest continuous imaginary boundary which can be drawn to encompass all known sites of occurrence of a species.

Table 1
Sites for each species, the number of burnt quadrats monitored after each fire, and the fire event in which they were burnt, for the three study species. The sites for *L. exolasius* are located in Heathcote National Park (NP) and are approximately 1.5 km apart, while the *L. esquamatus* sites, also located in Heathcote NP, are adjacent. The L. *setiger* sites are in Royal NP and approximately 4 km apart. HR denotes a prescribed hazard reduction burn and WF denotes wildfire.

Study species	Number of sites	No. of quadrats monitored and season of burn	Seedling emergence after each fire (seedlings per m^2)
L. exolasius	Site 1 – Dingo	20 (winter 1999) HR	2.03 ± 0.23
		24 (summer 2001/02) WF	5.62 ± 0.73
	Site 2 – Lake Eckersley	15 (summer 2001/02) WF	5.15 ± 0.91
L. esquamatus	Site 1 – Sarahs 1	10 (winter 1999) HR	13.6 ± 1.69
		10 (summer 2001/02) WF	
	Site 2 – Sarahs 2	8 (winter 1999) HR	5.60 ± 1.72
		10 (summer 2001/02) WF	10.89 ± 3.17
L. setiger	Site 1 – Flat Rock Ck	10 (summer 2001/02) WF	3.40 ± 0.62
	Site 2 – Winifred Falls	10 (summer 2001/02) WF	4.30 ± 1.16

2.2. Background data

Reproductive attributes, including fecundity, seed viability, seed bank longevity, seed dormancy, germination, seedling survival and growth were collated from the literature and compared between all three species to identify limiting factors. Information on the habitat and substrate preferences of the study species, population structure, seed dormancy, seedling emergence phenology, seed bank longevity and seed viability were also included.

2.3. Study sites, habitat attributes and plant fecundity

Experimental data were collected from study sites located in the southern Sydney region, within Royal (34° 03′S, 151° 03′E) and Heathcote (34° 07′S, 150° 58′E) National Parks. The climate is temperate with no dry season (using the Köppen classification system). Average annual rainfall for the area is approximately 1050 mm distributed relatively evenly throughout the year, with the four highest monthly averages occurring in January, March, June and November. Average temperatures (maximum/minimum) are approximately 27/18 °C and 16/6 °C in summer and winter respectively.

A 30 m × 30 m plot was marked out at two study sites for each species. At each plot, the type of vegetation, slope and aspect were recorded. All individuals within the plots, covering a range of size classes, were tagged using stainless steel wire stakes with numbered brass tags. For each tagged plant, height (or stem length if not vertical), canopy area (calculated as an ellipse from two measurements at right angles) and the presence or absence of buds or flowers were recorded to estimate fecundity of mature populations during late spring. To enable comparisons between sites and species, the numbers of fruit per 0.1 m^2 of canopy were calculated for each plant. Data were tested for homogeneity of variance using Levene's test. Comparisons were conducted using a two-factor nested analysis of variance (ANOVA), with species treated as a fixed factor and site as a random factor, using SYSTAT.

For each species, seedling survival and growth experiments were designed so that plots at each of the two sites were burnt during a summer wildfire in 2001/02. Up to 25 permanent 1 m × 1 m quadrats were located under or near canopies of mature individuals within each plot, as seedling emergence had previously been observed occurring primarily within a few metres of adult canopies. Nearby (or adjacent) plots to the above summer wildfires had been burnt by a prescribed winter fire in 1999, at a single site for both *L. exolasius* and *L. esquamatus*. The summer wildfire was of very high intensity, occurring during extreme fire weather conditions, while the prescribed winter hazard reduction burn was of much lower intensity. However the quadrats observed after both fires had all been completely scorched. Total number of quadrats followed at each site, and the season of burn, are shown in Table 1.

2.4. Post-fire seedling survival and early growth

After fire, quadrats were inspected regularly for signs of seedling emergence (Ooi et al., 2004). Once emerged, all seedlings within quadrats were tagged. Time of emergence and seedling height were recorded upon tagging. Survival and height were subsequently recorded at the end of each summer and each winter for four years, as this was considered the time most likely for mortality to occur. Seedling survival and seedling heights were analysed at the end of the fourth summer using SYSTAT. Due to a small number of seedlings surviving in some plots, I first used using a one-factor ANOVA comparing seedling survival among species after four years (no differences found between species $F_{2,3} < 0.06$, $P > 0.940$). However, scrutiny if the data suggested there was large variation between sites for each species, so to test for possible site effects, a two-factor ANOVA without replication, with year and site as factors, was used. This approach does not allow testing of significance of the interaction and a cautious approach is recommended for testing the significance of main effects (Zar, 1984). The significance levels were therefore increased to 0.01.

2.5. Primary juvenile period

Seedlings were tagged and survival and growth followed from 2002 to 2016 after the 2001/02 summer fire to determine primary juvenile period. This was assessed each year for the first four years, and then in 2006, 2009, 2012, 2014 and 2016. The time taken for tagged individuals to flower was recorded. Data from occasional years were missed, however multiple years over time were still recorded until maturity for all species. The total number of individuals assessed changed over time due to mortality, with the original number of seedlings tagged ranging from 33 (*L. exolasius*) to 151 (*L. esquamatus*). By the time approximately 80% of the population was in flower, total number of individuals surviving varied among species (*L. exolasius*, 7–12; *L. setiger*, 8–13; *L. esquamatus* 12–55). Data were analysed using a binomial Generalised Linear Mixed Model (GLMM), with site included as a random factor, to determine if the time taken to mature differed between species. The logistic models fitted for each species were used to estimate the time taken for 50% and 80% of the population to reach maturity (i.e. flowered). Analyses were conducted using the lmer4 package in R (R Core Team, 2015).

2.6. Comparison of growth and primary juvenile period: winter vs summer fire

The effect of different fire seasons on seedling survival and growth was also investigated. The prescribed winter fire in 1999 that had burnt a single site for both *L. exolasius* and *L. esquamatus* meant that within-site comparisons could be made for these species after this fire and the 2001/2 summer wildfire event. Growth was followed for 16 years after the winter fire (seedlings emerged in 2000) and 14 years after the

summer fire (seedlings emerged in 2002), and primary juvenile period compared. Heights for each species were measured until all plants had reached maturity (approximately 4 years for *L. esquamatus* and 14–16 years for *L. exolasius*). A binomial Generalised Linear Model (GLM) was used to compare primary juvenile period after fire occurring in different seasons. The time to 50% and 80% of the population reaching maturity was estimated from the logistic model. A previous study (Ooi, 2010) reported some results from the winter fire for *L. esquamatus*, and was used in the interpretation of the current study. The effect of fire season on reproductive output was also estimated for *L. exolasius* by comparing canopy area for plants emerging after post-winter and post-summer burns.

3. Results

3.1. Comparison of background data

The collation of background data revealed a number of similarities between species. All species occur within the temperate climate zone, with no seasonal rainfall pattern. The two common species extend into regions with warmer (north) and cooler (south and/or higher altitude) overall temperatures. All species occur on similar low nutrient soils. They also occur in similar woodland habitats, although *L. esquamatus* is more dominant in heath than woodland and *L. exolasius* is restricted mainly to rocky areas near creeks and rivers (Table 1).

Although diaspore weights differ amongst species, seed weights (embryo and endosperm) were very similar, as are seed embryo morphologies (Table 2). All species displayed high levels of fecundity. *Leucopogon esquamatus* produced significantly more fruit per canopy area than the other two species ($F_{2,4} = 32.624$, $P = 0.004$), however, mean canopy area of mature *L. esquamatus* individuals was also smallest by at least an order of magnitude (Table 2). As a result, the overall production of seeds per plant varies little between the three study species. For each species, there were no significant differences found between study sites ($F_{3,47} = 0.398$, $P < 0.755$). Flowering phenology and likely pollinators are similar due to very similar flower morphology, as are the seed maturation times. Seed viability is also high for all species (Table 3), and consistently highest for the rare *L. exolasius*.

All three species have been classified as morphophysiologically dormant and require stratification at seasonal temperatures to overcome dormancy (Ooi et al., 2006a). Emergence in the field is therefore seasonal, with seedlings appearing at the same time of year (peaking in autumn/early winter), even if there is significant rainfall at other times of the year. Recruitment has been recorded to mainly occur after fire with seedling emergence still restricted to same emergence season (Table 3). Some inter-fire recruitment had also been recorded (Ooi et al., 2006b).

Two bird species, the Yellow-tufted Honeyeater (*Lichenostomus melanops*) and the Pied Currawong (*Strepera graculina*), were observed taking fruit from plants of the two fleshy-fruited species, *L. exolasius* and *L. setiger*. No birds were observed taking *L. esquamatus* fruit from plants (MKJ Ooi, unpubl. data). Emus (*Dromaius novaehollandiae*) were identified from the literature as a species that had a preference for drupaceous fruit of *Leucopogon* and other Ericaceae (Keighery, 1996; Quin, 1996; McGrath and Bass, 1999; Calviño-Cancela et al. 2006). Numbers of ericaceous fruit found in emu scats, studied in both eastern and south-western Australia, were orders of magnitude greater than that of any other species.

3.2. Early seedling growth and survival

While there was no difference found between species for the number of seedlings survived at the end of four years, results indicated large differences between sites for *L. setiger* and *L. esquamatus* ($P < 0.001$), but not for *L. exolasius*. With regards to seedling heights, *Leucopogon esquamatus* was significantly smaller than the other two species after 4 years growth ($F_{2,164} = 7.062$, $P = 0.001$) (Table 3).

3.3. Primary juvenile period

There was a significant effect of species on primary juvenile period ($\chi^2 = 504.24$, $P < 0.001$). All species differed significantly from each other ($P < 0.001$) (Fig. 1). *Leucopogon exolasius* was slowest to mature, taking almost 10 years for 50% of the population to flower, and over 11 years for 80% (Table 3).

3.4. Comparison of growth and primary juvenile period: winter vs summer fire

Post winter fire cohorts were either slower to grow or reach maturity. For L. *exolasius*, plant growth was slower (Fig. 2), with heights of post winter fire cohorts remaining smaller at 16 years post-fire, even compared to post summer fire cohorts that were only 14 years old. This is supported by data from a previous study (Ooi, 2010), which showed this same pattern of growth for *L. exolasius* in the first four years post-fire. Time to maturity did not differ between post summer and winter fire *L. exolasius* cohorts ($\chi^2 = 2.798$, $P = 0.094$), although estimates of time to flowering from the logistic models were still slower for post

Table 2
Comparison of species distribution, habitat and morphological traits for the three study species. Data are based on observations and other literature sources (where references are cited).

	Leucopogon exolasius	*Leucopogon setiger*	*Leucopogon esquamatus*
Geographic distribution (km^2)	230–477	> 40 000	> 250 000
Climate zones	Temperate with no dry season, warm summers	Temperate with no dry season, mild – warm summers	Temperate with no dry season, mild – hot summers
Habitat[abc]	Woodland, slopes near creeks, rock outcrops	Woodland	Heath and woodland
Substrate[abc]	Sandy soils, low nutrient	Sandy soils, low nutrient	Sandy soils, damp or skeletal, low nutrient
Habit (height range)[bc]	Shrub (1–2 m)	Shrub (1–2 m)	Shrub (0.6–1 m)
Mean canopy area of mature plants (m^2) (± SE)	1.18 ± 0.29	0.85 ± 0.13	0.01 ± 0.002
Mean no. fruit per 0.1 m^2 canopy area (± SE)	8.4 ± 3.4	16.9 ± 4.4	439.3 ± 115.0
Mean diaspore mass (mg)	13.1	10.9	4.9
Mean seed mass (mg) (embryo + endosperm)	1.5	1.4	0.9
Embryo morphology[d]	Underdeveloped linear	Underdeveloped linear	Underdeveloped linear

References used.
[a] Fairley and Moore (1989).
[b] Harden (1992).
[c] Benson and McDougall (1995).
[d] Ooi et al. (2006b).

Table 3
Comparison of phenological and life-history traits, and demographic responses for the three study species. Data are based on observations and other literature sources (where references are cited). Primary juvenile period was calculated from logistic models (see Fig. 1).

	Leucopogon exolasius	*Leucopogon setiger*	*Leucopogon esquamatus*
Fire response[a]	Obligate seeder	Obligate seeder	Obligate seeder
Flowering times	July–October	July–October	August–September
Flowers (pollinators)	Unspecialised (bees, flies, butterflies)*	Unspecialised (bees, flies, butterflies)*	Unspecialised (bees, flies, butterflies)*
Seed maturation	October–December	October–December	November–December
Seed viability[b]: 2000	88.90 ± 2.20	59.50 ± 2.42	56.00 ± 2.30
2002	92.33 ± 1.33	83.33 ± 4.91	61.67 ± 2.33
Dispersal mechanisms	Vertebrate and ant	Vertebrate and ant	Ant
Field germination[c]	May–September	May–September	April–August
Primary juvenile period (years)			
- for 50% of population	9.96	6.66	2.54
- for 80% of population	11.19	7.57	3.20
Estimated mean seed bank half-life (years)[c] (range of 1 S.E in brackets)	5.45 (4.22–7.73)	4.44 (3.07–8.06)	3.47 (2.67–4.95)
% seedling survival 4 years post-fire; range over two sites. (N = number of seedlings originally tagged)	24–47% (N = 152 & 33)	23–42% (N = 37 & 53)	15–43% (N = 91 & 128)

NB. * denotes inferred from observations and literature (Keighery, 1996).
References used.
[a] Ooi et al. (2006a).
[b] Ooi et al. (2007).
[c] Ooi et al., 2004.

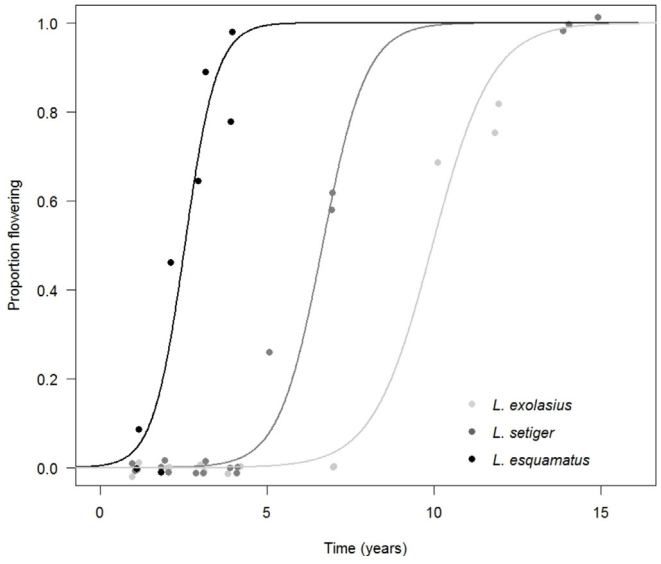

Fig. 1. Proportion of tagged plants flowering as a function of time since fire for *Leucopogon exolasius*, and two common congeners *L. setiger* and *L. esquamatus*. Plots were burnt in the summer of 2001/02. Species are represented by different colours indicated in the key.

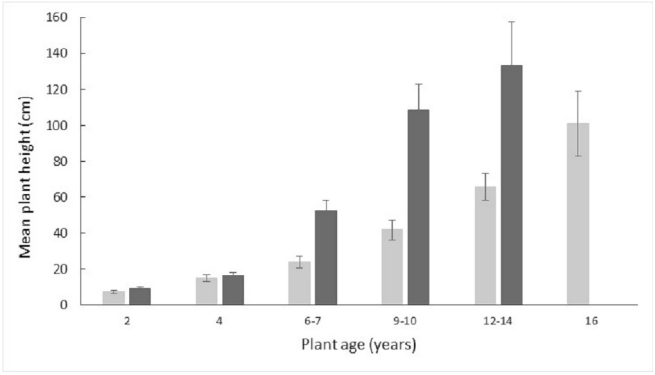

Fig. 2. Mean seedling heights of *Leucopogon exolasius* over a 16-year time series after a winter fire ( ) and a summer fire ( ). In classes where there are a range of ages, post-summer fire plants are always slightly older (e.g. at the 6–7 year age class), post winter fire plants are 6 years old and summer fire plants 7 years old. Bars represent 1 standard error. NB Growth was followed for 16 years after the winter fire (seedlings emerged in 2000) and 14 years after the summer fire (seedlings emerged in 2002).

winter fire cohorts (time for 50% population to reach maturity 9.97 (summer fire) vs 11.35 years (winter fire) years; for 80% of the population this was 11.51 (summer fire) vs 12.89 (winter fire) years) there was a large difference in the size of canopy area at 14–16 years post-fire (summer fire 0.49 ± 0.19 m^2; winter fire 0.18 ± 0.05 m^2). The relationship between canopy area and seed production would mean lower reproductive output from post-winter fire.

For L. *esquamatus*, time to flowering was significantly slower for seedlings emerging after a winter fire, than those that emerged after the summer fire (Fig. 3) ($\chi^2 = 14.831$, $P < 0.001$). Estimates of time to flowering from the logistic models showed a delay of more than one year (time for 50% population to reach maturity 3.12 (summer fire) vs 4.55 years (winter fire) years; for 80% of the population this was 4.09 (summer fire) vs 5.51 (winter fire) years). Growth rates for *L. esquamatus* were previously reported to not differ between fire season cohorts (Ooi, 2010).

4. Discussion

Ecological comparisons of the three study species highlighted two factors; a long primary juvenile period specific to the threatened species *L. exolasius* and an innate seasonal requirement of dormancy and germination mechanisms for all species, both traits that could potentially influence rarity. Changes to fire season were found to increase primary juvenile period. Changes to fire season can therefore interact with fire frequency and influence population persistence. This has broad implications for many species from fire-prone plant communities and highlights the need to understand the consequences of future changes to the fire regime.

In fire-prone regions, the time taken for seedlings to reach maturity is critical for obligate-seeding species. Adult plants are killed by fire and seed bank replenishment is dependent primarily on the post-fire cohort producing seeds prior to the next fire (Auld, 1987; Bradstock and Kenny, 2003). In our study, the majority of *L. esquamatus* and *L. setiger* plants had reached maturity within approximately three years and seven years respectively, after summer wildfires. The majority of *L.*

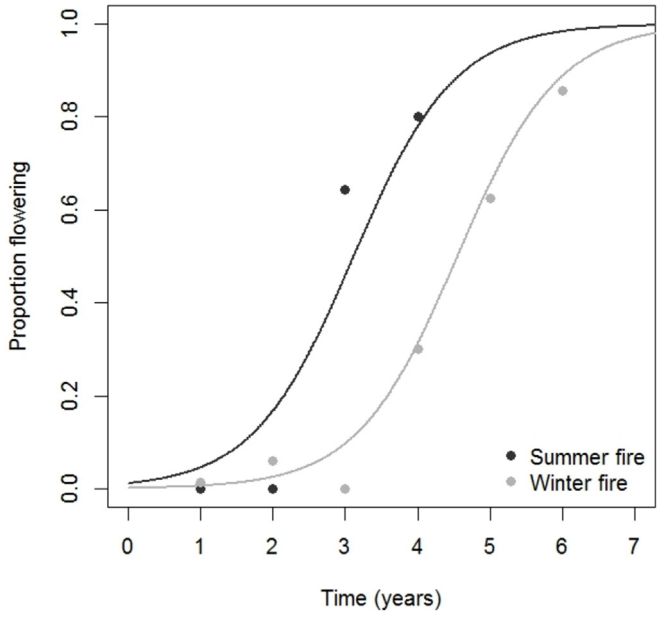

Fig. 3. Proportion of L. *esquamatus* plants flowering as a function of time, for cohorts emerging after either a summer or winter fire.

exolasius plants did not reach maturity until approximately 11 years post-fire. Results from studies of over 40 other obligate-seeding shrub species in the region, found only four with primary juvenile periods longer than six years, and all three had matured in less than 6 years at some sites (Benson, 1985; Keith, 1996; Bradstock and Kenny, 2003; Kubiak, 2009). The primary juvenile period of *L. exolasius* is therefore particularly long by regional standards. Obligate seeders with long primary juvenile periods are particularly at risk to an increased fire frequency because post-fire recruits are killed before they reach maturity.

As observed during the course of this study, both the *L. setiger* sites and one of the *L. esquamatus* sites were burnt by wildfires after only a seven year interval, which is at the lower limit of fire-free intervals for this region (Bradstock et al., 1998). We suggest that occasional short interval fires, as part of the natural regime in the past, have limited the extent of *L. exolasius* populations. Projected increases brought about by increasing numbers of managed fires, and also climate change (McLoughlin, 1998; Williams et al., 2001; Hughes, 2003; Cary et al., 2006), are likely to place obligate-seeding species with long primary juvenile periods such as *L. exolasius*, at even greater risk.

The habitat of extant *L. exolasius* populations provides further evidence that slow maturation and a lack of resilience to shorter interval fires may have limited this species distribution. All three study species occur on similar low nutrient soils that extend beyond the realised range. However, *L. exolasius* occurs almost exclusively on rocky riparian sites (Fairley and Moore, 1989; Benson and McDougall, 1995; Ooi et al., 2006b). This type of habitat can provide areas of fire refugia (Pettit and Naiman, 2007), as has been found for *L. exolasius* (Ooi et al., 2006b) and a number of other south-east Australian species (Clarke, 2002; Collette and Ooi, 2017), effectively reducing the frequency of fire faced by resident plant populations. Gill and Bradstock (1995) suggested that rare obligate-seeding plant species are concentrated in parts of the landscape where fires are less common. Although the common congeners *L. setiger* and *L. esquamatus* can occur in rocky habitats, they are not restricted to them (Ooi et al., 2006b).

Morphophysiological dormancy (MPD) was also common to all study species (Ooi et al., 2006a), and could represent a further limiting factor for *L. exolasius*. MPD requires (usually) seasonal temperature stratification or after-ripening to overcome physiological dormancy, as well as growth of the underdeveloped embryo (morphological dormancy), both which can delay germination and lead to a seasonal germination requirement. This seasonal emergence has also been identified in a number of other dominant physiologically dormant genera in these systems including *Boronia* and *Asterolasia* (Mackenzie et al., 2016; Collette and Ooi, 2017). An innate seasonal requirement for germination meant that seedling emergence in the field is seasonal, with seedlings appear at the same time of year (peaking in autumn/early winter) even if significant rainfall occurs at other times of the year. Recruitment mainly takes place after fire but seedling emergence is still restricted to the same season (Ooi et al., 2004). *Leucopogon* emergence can therefore be delayed in relation to fire, depending on the season of the fire event. After a winter fire, Ooi (2010) found that emergence of *L. exolasius* and *L. esquamatus* was delayed by almost 12 months.

This current study confirmed that delayed emergence relative to fire caused slower growth and potentially reduced seed production of *L. exolasius* (smaller plants produce fewer seeds), which would reduce the capacity for fast seed bank recovery post-fire. Several mechanisms could contribute to a reduced rate of growth. Earlier emergence of co-occurring species which do not have a seasonal requirement could lead to *Leucopogon* being outcompeted for resources (Ooi et al., 2004). Changes to elements of the fire regime that interact with season may also impact growth. For example, soil heating from the implemented winter prescribed fire and the summer wildfire would be significantly different, having varying effects on physical, chemical and biological soil properties, with potential impacts on post-fire plant growth (Santin and Doerr, 2016). Further work is required to understand how shifts in fire season may impact vegetation recovery.

An increase in primary juvenile period would raise the chances of fire killing populations prior to maturation and seed bank replenishment. However, whilst significant, the amount of increase for the common species *L. esquamatus* still meant that a large proportion of populations were likely to reach maturity prior to subsequent fire, even in the event of a short fire-free period such as the seven year interval experienced during our study. Slower seedling growth for the rare species *L. exolasius* could increase the likelihood that immature populations would be killed, or that insufficient recovery of seed banks would occur, even under a more common 10 year fire interval, which occurs regularly under natural fire regimes. The potential negative effects of seasonal emergence on the common species studied could therefore be offset by the shorter primary juvenile period of *L. esquamatus*, and to a lesser extent *L. setiger*, whereas seasonal germination of the rare *L. exolasius* could exacerbate problems caused by an already long primary juvenile period.

Emergence of all three study species is delayed, particularly by winter, out-of-season fires. Co-occurring shrub species without seasonal germination requirements germinated rapidly after fire (within 1 month), and grow more quickly and survived to higher proportions than their seasonally emerging counterparts (Ooi et al., 2004; Ooi, 2010). Because L. *exolasius* persistence appears to be bound tightly to fire frequency and season, it is likely that its ability to persist in the future will be strongly tested by changes to the fire regime. The impacts of implemented fires and the effects of climate change are both forecast to promote more frequent fires (Williams et al., 2001; Cary et al., 2006). These changes represent significant threats to *L. exolasius*, and management should aim to reduce the frequency of fire faced by these populations, as well as by other obligate-seeding species in the region with long primary juvenile periods. The effects of changes to the peak fire season, which has already begun particularly near the urban interface (e.g. McLoughlin, 1998), could also increase the level of threat faced by all *Leucopogon* species. This potential threat provides land managers with the challenge of incorporating aspects of the fire regime beyond frequency alone, and needs to be considered further when developing management guidelines for a range of species with seasonal dormancy and germination requirements. Understanding the impacts of the timing of implemented fires is relevant for managers of fire-prone

plant communities throughout the world (Liu et al., 2005).

Acknowledgements

This study was funded under the National Environmental Science Programme's (NESP) Threatened Species Recovery Hub (Project 1.3) and from support by the NSW Office of Environment and Heritage's 'Saving our Species Programme'. Thanks to Lachlan Wilmott (OEH Illawarra) for assistance in the field, and Rob Whelan and Tony Auld for comments on an earlier version of this manuscript.

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